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## The Structure, Distribution, and Taxonomic Importance of Trichobothria in the Miridae (Hemiptera)

RANDALL T. SCHUH<sup>1</sup>

### ABSTRACT

Trichobothrial structure, function, and occurrence are reviewed for the Arthropoda. A survey is made of all setae that have been classified as trichobothria within the Hemiptera. Trichobothria are recorded for the first time from the mesofemora and metafemora of the Miridae. Scanning electron photomicrographs showing detailed structure and drawings of the numbers and locations of these specialized setae are presented for representatives of the majority of the currently recognized tribes in the family. Within the

limits of current knowledge the trichobothria in the various taxa of Miridae are homologized and a numbering scheme is presented. It is suggested that the hypothetical primitive number for the mesofemur is six and that for the metafemur seven or eight. The phylogenetic significance of the trichobothria in the Miridae is discussed, with the conclusion that they constitute an autapomorphic character and that the Miridae, including the Isometopinae, represent a monophyletic group.

### INTRODUCTION

The present paper has its origin in an encounter with some long setae on the ventral surfaces of the femora of the middle and hind legs of certain species of Miridae while, during a previous study, I was searching for new taxonomic characters in the family (Schuh, 1974). Access to a Scanning Electron Microscope (SEM) provided an improved opportunity for further investigation of these interesting setae, which actually proved to be trichobothria.

The SEM photomicrographs were made from specimens generally killed in cyanide and received no other special preparation. The speci-

mens were plated with carbon and gold-palladium. Reproduction of all photographs is at the same scale with the magnification indicated, so that relative sizes can be determined. Maps of trichobothrial patterns were made with a Leitz dissecting microscope or Wild M-20 compound microscope and camera-lucida, aided by SEM observations; the femora are not reproduced to the same scale in different species because of the great variation in their absolute size.

I thank Mr. Robert Koestler for his patience and expertise in making the SEM photographs; these were produced on a Cambridge Scientific

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Instruments Model S-4, purchased through a grant from the National Science Foundation. Drs. Pedro Wygodzinsky and Norman Platnick participated in many discussions and provided useful references. Miss Patricia Neary carefully typed and helped edit the manuscript.

### OCCURRENCE, STRUCTURE, AND FUNCTION OF TRICHOBOTHRIA

Trichobothria were first recorded in spiders by Dahl (1883), who called them "Hörhaare"; he later (1911) applied the term trichobothria, based on their structure, which consists of a very long slender seta (or "trich"), set in a cuplike depression in the cuticle or on a small dome (the "bothrium"). In addition to spiders, the presence of trichobothria has now been confirmed in Acari, Scorpionida, Pseudoscorpionida, and several other groups of arachnids, in Pauropoda, Symphyla, Collembola, Diplura, Thysanura, Microcoryphia, Blattodea, Orthoptera, Psocoptera and Hemiptera (for references see Hansen, 1917; Tullgren, 1918; Wygodzinsky, 1941; Tarman, 1961; Slifer, 1968; Haupt, 1970; Slifer and Sekhon, 1970; Gnatzy and Schmidt, 1971).

The taxonomic value of trichobothria has been demonstrated in several groups (for example, Tullgren, 1918; Schaeffer, 1966; Vachon, 1973), especially with reference to their numbers and spatial arrangement (chaetotaxy). Recently much interest has been shown in the functional nature of trichobothria, a subject that was first considered by Dahl, who played a violin in the presence of a spider trichobothrium and noticed that it vibrated, hence the term Hörhaare.

That trichobothria occur in so many unrelated groups of arthropods suggests that they are structures of similar functional type rather than of common origin. A brief review of the structure and function of trichobothria should therefore be instructive.

The external structure of the trichobothrium is generally that of the definition given above. The "trich" itself is usually longer than the surrounding setae arising from the cuticle and is not strongly tapered or obviously conical, as are the majority of the setae in arthropods. It is oriented at a more or less right angle to the cuticle, whereas most setae form an acute angle with the sur-

rounding body surface. In most Hemiptera so far examined, the trich is "fluted" longitudinally (fig. 8) and does not show the twisted structure of most investing hairs. Lawry (1973) noted that the femorotrochanteral trichs in the Gerridae are smooth (not fluted), although my observations on *Gerris remigis* Say, the same species examined by Lawry, show them to be weakly fluted. In some spiders, the trichobothria have short branches, a type of structure that might be termed "plumose" (see Christian, 1972; Platnick and Lau, 1975, fig. 6). Basally the trich is either straight or constricted (see figs. 9 and 76, respectively).

The bothrium has two rather obvious structural variations with a wide range of intermediates. The most common types are (1) those where the bothrium is a pitlike depression in the cuticle, as in many Miridae (see fig. 8) and (2) those where the bothrium is a raised domelike structure and may be surrounded by a cuticular investment (see fig. 9). The structure of the bothrium can be additionally complicated by the presence of a "trichoma," a structure referred to as the "maculae opacae" or "matten Flecke" by older authors; it consists of a group of spicules (fig. 74, etc.) or a modified cuticular area (fig. 5). Dräslar (1973) commented on the presence of a trichoma in mites, spiders, and scorpions, citing Tarman (1961), Hoffman (1965), and Christian (1971). The structures referred to by Dräslar are not termed trichomae by the authors he cited, however, and are actually quite different in structure than those found in the Hemiptera, the only place in which they are known, as far as I am aware.

The basal neural structure of trichobothria has been recently investigated by several authors. No single type can be defined, although there does seem to be a pattern in the mode of innervation and a certain uniformity within any given taxon.

A single neuron innervates the "filiform hairs" in certain Gryllidae (see Gnatzy and Schmidt, 1971; Edwards and Palka, 1974). There are two or three neurons in certain spider trichobothria (Görner, 1965). Tarman (1961) described mites as having five to 10 bipolar sense cells, and this number can range as high as 16, as recorded in *Scutigerebella* (Symphyla) by Haupt (1970). In many cases the trichobothria have a so-called

tubular body, which is apparently common to the innervation of the majority of mechanoreceptors (see Foelix and Chu-Wang, 1973). Gaffal and Hansen (1972) investigated the structure of non-trichobothrial mechanoreceptors on the antennae of *Dysdercus* (Pyrrhocoridae) and noted that they have a basal tubular body similar in structure to that found associated with trichobothria in Symphyla (see Haupt, 1970) and Araneae (*Tegenaria*) (see Christian, 1971).

In the Arachnida trichobothria are most common on the pedipalps, to which they are apparently restricted in the scorpions and pseudoscorpions, but they also occur on the walking legs in spiders. They are present on the abdomen in Collembola (Paclt, 1956). In the Diplura they are found in a fixed arrangement and number on the antennae (Wygodzinsky, personal commun.); at least certain Microcoryphia have trichobothria on either side of the ecdysial line on the mesothorax (Wygodzinsky, 1941); and in the Thysanura (*Ctenolepisma*) they are found on the antennae, cerci, and pseudocercus (Slifer and Sekhon, 1970). Wygodzinsky (personal commun.) noted that in the Diplura trichobothria are more numerous in cavernicolous species than in non-cavernicolous species, that in the Microcoryphia they are most common on species that live on rocks or cliffs and less so on species that are ground living, and that in the Thysanura they are more common in termitophilous species than in noninquiline forms.

In the Blattodea and Orthoptera, trichobothria (termed "filiform hairs" or "Fadenhaare" by some authors) are present on the cerci and apparently on the abdomen, in the Psocoptera on the paraprocts, and in the Hemiptera on the abdomen in the "trichophoran" families (i.e., Coreoidea, Pentatomoidea, Lygaeoidea, Pyrrhocoroidea) (Tullgren, 1918), on the mesofemora and metafemora in the Miridae, and in other locations in other families (see below). Schaeffer (personal commun.) noted that trichobothria are longer in those "trichophoran" families of Hemiptera that are ground living than in those dwelling on vegetation, something that can be observed by comparing a rhyparochromine lygaeid with a pentatomid or coreid.

The first suggested function for the trichobothria was that of sound reception; Schaeffer

(1966) considered this the most plausible function for Hemipteran trichobothria. Several workers have conducted experiments attempting to show a phonoreceptive function (see Haskell, 1956, for grasshoppers; Guthrie, 1966, for cockroaches; and Dräslar, 1973, for *Dysdercus*). None of these experiments have been conclusive, although the detection of air movements has been strongly indicated. Specific studies on the detection of air movements have been conducted by Hoffman (1967), Görner and Andrews (1969), Slifer and Sekhon (1970), and Edwards and Palka (1974). The results in all of these cases were positive. Görner and Andrews (1969) suggested that the trichobothria in spiders function as organs of "touch at a distance" ("Ferntastsinnesorgan").

Teyrovsky (1923) discovered trichobothria on the legs of the Gerridae. It now seems certain that these are important in determining the point of origin of ripples on the water surface film in association with prey capture (see Murphy, 1971; Lawry, 1973).

The function of the femoral trichobothria in Miridae discussed below is unknown. The idea of sound reception is one possibility, in that mirids are known to possess stridulatory mechanisms (Schuh, 1974; MS.). The nature of these structures as receptors of such sounds seems doubtful, however. They may have an analogous function to the trichobothria of the trichophoran Hemiptera, but even there, where some experimental data exist, exact function is still in doubt. A tactile role might be inferred in that the trichobothria are almost always longer than the other body hairs and project beyond them.

It is also possible that the trichobothrial function is of a more complex nature than has previously been suggested and cannot be categorized as strictly auditory or tactile. As indicated by Dräslar (1973) (see also discussion in Edwards and Palka, 1974), different trichs have different stimulus-response properties, possibly suggesting a multiple sensory role.

Although the trichoma is present in several unrelated groups, its function is unknown. It has been speculated that it is important in limiting the travel of the trichobothrium in any one direction, although no experimental evidence exists in support of this hypothesis. Edwards and Palka

(1974) noted that the socket of the filiform hairs in crickets limits excursion and gives these setae a preferred plane of travel.

### TRICHOBOTHRIA IN THE HEMIPTERA

If one is limited only to the consideration of the trichobothria on the abdomen of the trichophoran families of Hemiptera, no particular problems arise in recognizing the structures as such.

However, many other trichobothria-like setae exist within the order, and it soon becomes evident that strict definitions cannot be applied.

Table 1 indicates the occurrence of trichobothria in the Hemiptera. Only those families known to have trichobothria are listed; the following families have also been examined, however: Enicocephalidae, Dipsocoridae, Schizopteridae, Thaumastocoridae, Tingidae, Aradidae, Ochteridae, Gelastocoridae, Notonectidae, Nepidae,

TABLE 1  
Occurrence of Trichobothria in the Hemiptera

Family	Cephalic and Antennal Trichobothria	Pronotal and Scutellar Trichobothria	Abdominal Trichobothria	Femoral Trichobothria
Saldidae	Cephalic: 3 pairs, without trichoma; all genera (fig. 3)	—	—	—
Gerridae	Cephalic: 3 pairs, with trichoma (?), deeply recessed; all genera	—	—	10-20 on coxae, trochanters and femora (middle and hind legs); no trichoma present
Veliidae	Same as Gerridae	—	—	In some taxa
Mesoveliidae, Hydrometridae, related taxa	Same as Gerridae (fig. 1)	—	—	—
Nabidae	Cephalic: 1 or more pairs, usually without trichomae	Scutellar: number variable; with or without trichomae	—	—
Pachynomidae	—	—	1 pair laterally on sternites 7 and 8	—
Anthocoridae	—	—	Perigenital, some genera	—
Miridae	—	Pronotal: lateral in some genera (fig. 4)	—	2 to 9 on mesofemora and metafemora, usually with trichoma
Reduviidae	Antennal: variable number on segment 2	—	—	—
Lygaeoidea	Cephalic: 3 pairs, no trichoma; only in Rhyparochrominae	—	Laterally and mesially, with trichoma	—
Pyrrhocoroidea	—	—	Laterally and mesially, with trichoma	—
Coreoidea	—	—	Laterally, without trichoma	—
Pentatomoidea	—	Pronotal: lateral in Cydnidae	—	—

Naucoridae, Belostomatidae, and Corixidae. Those setae included in the table are any which roughly fit the definition given above or that have been referred to in the literature as trichobothria. A rather broad range of setal structure and location exists. The recognizable structural types can be defined as follows for purposes of convenience: (1) those with a simple base, somewhat resembling that of a seta, although with a generally slender trichlike hair (figs. 2, 3); (2) those with an obvious bothrium, either recessed or not, and lacking a trichoma (fig. 55); (3) those with a bothrium surrounded or obscured by a cuticular dome (fig. 9); and (4) those with the bothrium more or less sunken into the surrounding cuticle and with a trichoma (figs. 8, 51, 52, 78). Trichobothria can be classified further as follows, in terms of their location: (1) antennal, (2) cephalic, (3) pronotal, (4) scutellar, (5) abdominal, (6) femorotrochanteral; examples are shown in figures 1-12. Although not all structural types are found in all locations, several different combinations are possible.

Before proceeding to the discussion of trichobothria in the Miridae, I shall discuss the phylogenetic implications of the trichobothria in the Hemiptera as a whole.

Three pairs of trichlike setae occur on the head in the families Saldidae, Nabidae, the lygaeid subfamily Rhyparochrominae, and in the gerroid-complex of families (including Gerridae, Veliidae, Mesoveliidae, Hebridae, Hydrometridae, and a few isolated genera, sometimes placed in distinct families). These have not been used in establishing classifications of the Hemiptera, although the similarity among the four groups relative to their possession of cephalic trichobothria is rather remarkable, as noted by Cobben (1968).

Morphologically two obviously distinct types are present under the title cephalic trichobothria. The simplest type is that found in the Rhyparochrominae, Nabidae, and Saldidae. Here the bothrium is a small raised area on the cuticle. The trich in the Rhyparochrominae [see *Valtissius diversus* (Distant), fig. 2] is not of the fluted type found in most Miridae and certain other groups, nor is it twisted as are most investing hairs, but has a pyramidal pattern formed by the "setal sub-units." In some Nabidae the trichs are very heavy and appear as conventional setae,

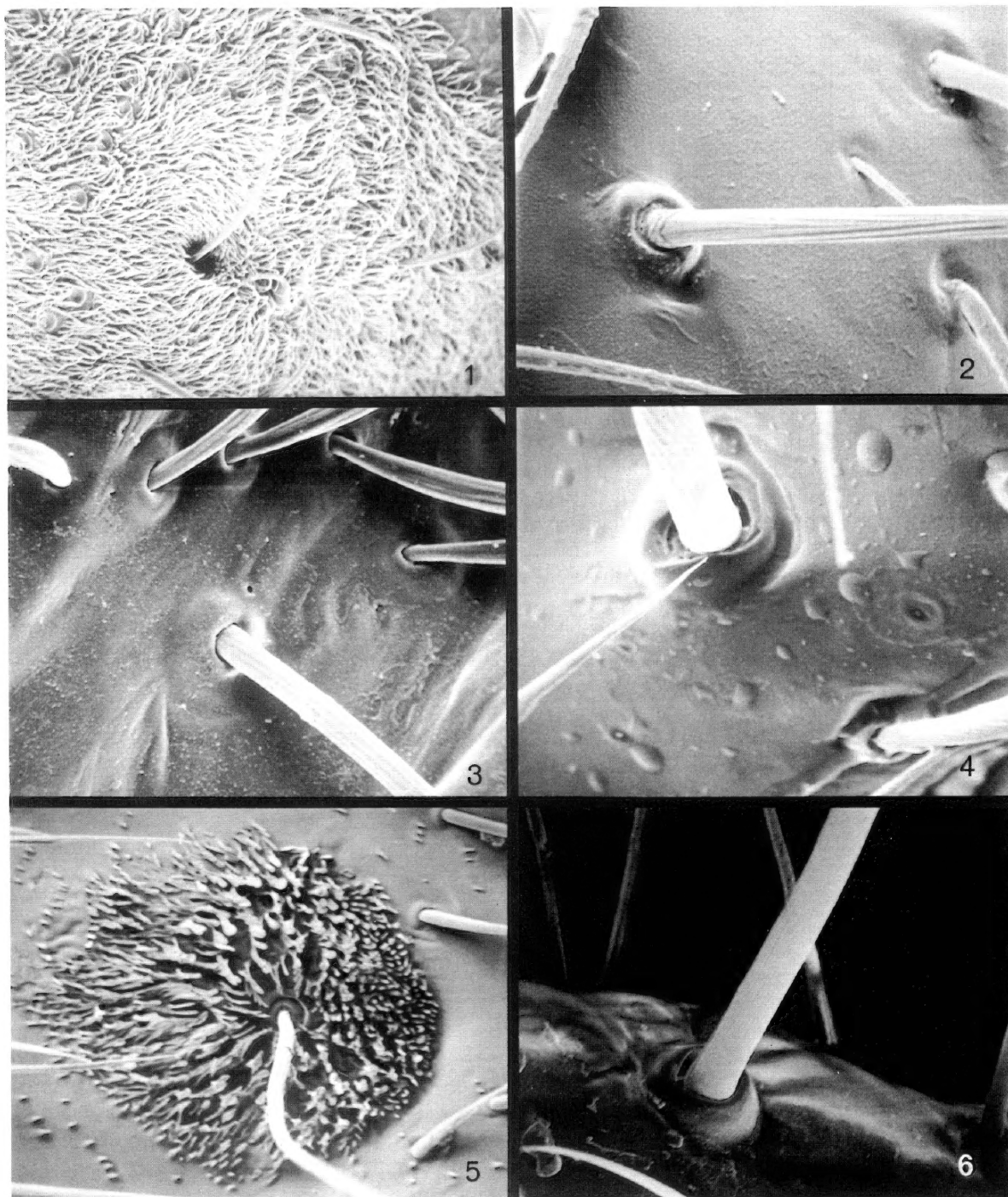
whereas in *Nabis subcoleoptratus* Kirby at least one pair of these cephalic hairs is very fine and has a trichoma surrounding it (the cephalic trichobothria in the Nabidae have not been studied with the SEM). In *Micracanthia schuhi* Lattin (fig. 3) the trich is fluted, with the flutings running all the way to the base.

In the Hydrometridae, Hebridae, Gerridae, and Veliidae, the bothrium is sunken into the head and the basal portion of the trich and the bothrium are not readily visible. The surface of the body of this group of bugs is often in large part covered with a fine pile, which is important in preventing wetting; it is therefore difficult to say whether a trichoma exists or not.

Based on the apparent distant relationships of the taxa that possess cephalic trichobothria, especially the Rhyparochrominae relative to the other mentioned groups, it would seem that the head trichobothria have a strong functional role, and that they have evolved more than once. The habits of the bugs, ranging from free-living species, such as the nabine Nabidae, semiaquatic littoral forms such as the Saldidae, water surface forms in the gerroid families, and litter-dwelling forms in the Rhyparochrominae (Lygaeidae) and Prostemmae (Nabidae), do not suggest that any particular life mode is associated with the presence of cephalic trichobothria. Certainly, this is a fertile area for more comparative morphological and physiological research.

Cobben (1968) suggested the study of cephalic trichobothria in nymphal forms to assess ontogenetic changes, an idea of unquestionable merit; however, whether his assumption that Amphibicorisan-type bugs can be regarded as directly ancestral to other Hemiptera, especially in light of the methods of phylogenetic systematics, is doubtful. Also, even if the nymphs of many Hemipteran taxa possessed cephalic trichobothria, this would almost certainly have to be regarded as a primitive character and therefore would not necessarily form the basis for relating those families in which they are possessed by the adults.

Antennal trichobothria have been recorded on the second antennal segment of members of the genus *Belminus*, a triatomine reduviid (Herrer, Lent, and Wygodzinsky, 1954). Similar trichobothria are present in other Triatominae, and



FIGS. 1-6. Trichobothria of Hemiptera, scanning electron photomicrographs. 1. *Hydrometra* sp. (Hydrometridae), anterior cephalic trichobothrium, 1050X. 2. *Valtissius diversus* (Distant) (Lygaeidae), middle cephalic trichobothrium, 2080X. 3. *Micracanthia schuhi* Lattin (Saldidae), cephalic trichobothrium, 2600X. 4. *Paramixia australis* Schuh (Miridae), pronotal "trichobothrium," 2600X. 5. *Paragonatus divergens* Distant (Lygaeidae), lateral abdominal trichobothrium, 1250X. 6. *Lasiochilus* sp. (Anthocoridae), perigenital "trichobothrium," 2400X.

also in the subfamily Piratinae. Although they might be expected to occur in other reduviids, they are not known from other families of Hemiptera.

"Putative" trichobothria are known on the pronota of some mirids and probably in other groups (see Cydnidae). In those mirids examined (see fig. 4 of *Paramixia*), the structure of the seta is not typical of most known trichs in that it is twisted and rather stout. Nonetheless, the basal structure might be interpreted as a bothrium.

Scutellar trichobothria are present in the Nabidae but in no other Hemiptera. Carayon (1970) has presented some excellent SEM photos of these in the genus *Alloeorhynchus* Fieber and has recorded their presence in other prostemmine nabids, noting that they vary in number from two to 14, depending on the genus, and that they are present on the lateral dorsal abdominal surface in the nymphs, whereas they occur on the scutellum in the adults. The bothrium is strongly recessed in *Alloeorhynchus*, appears to have a trichoma, and is reminiscent of those of the cephalic trichobothria in the gerroid families. Carayon (1970) said scutellar trichobothria are not present on the Nabinae; however, my observations suggest that analogous setae are present in at least some cases, although without a definite trichobothria-like structure. This would suggest the multiple origin of trichobothria, as appears to be the case with the cephalic trichobothria discussed above.

Perigenital setae of a trichobothria-like nature occur in the Anthocoridae (fig. 6) and were termed "macrochètes" by Carayon (1972b). It appears that no other trichobothria-like setae occur in the family. Even the perigenital trichs are lost in the ectoparasitic Cimicidae, which belong to the same clade as the Anthocoridae. Carayon and Villiers (1968) recorded varying numbers of true trichobothria on the abdominal sternites in the Pachynomidae; possibly analogous setae also occur in some Nabidae (see Carayon, 1970).

Trichobothria on the abdomen, aside from those just mentioned, are known only in the trichophoran families, occurring laterally, and in some cases mesially on the abdominal venter. In many cases these have a well-developed trichoma (fig. 5). The Hemiptera, as can be seen, have a plethora of trichobothria, and it may be that in

more than one case they are of independent origin but conform to some primitive setal arrangement for nontrichobothria. Only careful comparative morphological studies can test such a hypothesis.

#### FEMORAL TRICHOBOTHRIA IN THE MIRIDAE

Femoral trichobothria, which are the primary concern of this study, were formerly known only in the Gerridae (see Teyrovsky, 1923; Lawry, 1973). Now their presence is also confirmed in the Miridae.

In the Miridae the trichobothria are present only on the mesofemora and metafemora, whereas in the Gerridae they also occur on the coxae, trochanters, and tibiae of the middle and hind legs (see Lawry, 1973). No sexual dimorphism is obvious in the trichobothria in those taxa so far examined. The trichobothria are present in the same location in both the nymphs and adults. The general location on the femur is ventral, although certain trichobothria are often placed laterally. The tendency is toward a well-developed spinose trichoma, something that is not known in the same form in any other arthropods that possess trichobothria, although trichomae of a somewhat different form exist in the trichophoran Hemiptera (see fig. 5 and above). The trichoma tends to be of the same form for all trichobothria in a given species, varying only in size. In general the trichobothria in the Miridae are small and difficult to see with a dissecting microscope; thus their study necessitates the use of slide mounts and is greatly facilitated by the scanning electron microscope. Usually the trichobothria can be recognized with a dissecting scope by the length and erect nature of the trichs and occasionally by the texture of the trichoma in those cases where it is well developed and spread out over a reasonably large area of cuticle; where the trichoma is reduced or compact it is virtually impossible to locate the trich bases. Under the SEM the sunken bothria produce a strong shadow effect (see fig. 53) and are thus easily recognizable, whereas the bothria that are not sunken and lack a trichoma (fig. 55) are often difficult to see even under ideal circumstances.

Trichobothria are known in all Miridae that have been examined, but they do not seem to be

present on the legs of the taxon which is probably the sister group of the Miridae, namely the Anthocoridae (based on the presence of a cuneus in both groups), nor are they present in the Nabidae, which have a more primitive complex of characters than the Miridae but appear to belong to the same clade (see Schuh, 1974). Thus the femoral trichobothria can be considered as apomorphic, which suggests that the Miridae including the Isometopinae form a monophyletic group. The latter group has not been included in the Miridae by many authors (e.g., Carvalho, 1952; but see McAtee and Malloch, 1932, and Carayon, 1958) because its members have ocelli, which are obviously plesiomorphic in the Hemiptera.

A summary of the trichobothrial condition for all the higher taxa of Miridae that have been examined, either with light microscopy or the SEM, is given below. Taxa that have been examined in detail with the SEM or slide mounts are listed; in most cases additional species were examined less intensively to help confirm the existence of numbers and patterns. Figures 1-84 show the trichomae and bothria and the number and arrangement of the trichobothria in representatives of most mirid subfamilies and tribes; the Palauocorinae Carvalho have not been examined. In the drawings trichobothria with a trichoma are indicated with two concentric circles at their bases, those without a trichoma with only a single circle representing the bothrium. Trichobothria on the opposite side of the legs are indicated by dotted lines. The classification followed is basically that of Carvalho (1952) with some modifications based on my own work (Schuh, 1974).

*The Trichs.* The trichs of mirids all show the same basic fluted structure. In some cases the flutes run to the point of insertion in the bothrium (fig. 77), or nearly so (fig. 74), whereas in others they stop short of this and the basal portion of the trich is unfluted and constricted (fig. 78). The length of the trichs varies considerably within a given individual, and homologous trichs may be of significantly different lengths in different taxa. In the drawings that accompany this discussion no attempt has been made to show absolute lengths, but relative lengths for any given leg are reasonably accurate.

*The Trichoma and Bothrium.* The trichoma is

a characteristic structure in most mirid trichobothria. Its derivation in some cases appears to be simply a specialization and "concentration" of the spicules that commonly invest the body surface. In other cases the body is generally nude and there are no existing structures from which the trichoma could be obviously derived.

In some mirid taxa the trichoma is completely lacking (Monaloniini and Odoniellini), and in other cases it is absent from certain trichobothria only. The latter case is well represented by the genus *Austropsallus*, where SEM observations have been made. Figures 74 and 75 show trichobothria of *Austropsallus drakensbergensis* with and without trichomae. There seems to be little question that both setae are trichobothria, judging from their structure, although the bothria are somewhat different.

The trichoma often shows an asymmetrical orientation, as is especially obvious in the cases of *Pachymeroerus pilosus* and *Fulvius* (figs. 8 and 12, respectively). In the case of those trichs that are not oriented perpendicularly to the body surface, the trichoma and the trich have the same angularity.

The bothrium is sometimes sunken into the surrounding cuticle (fig. 52), and in many such cases the trichoma tends to be more compact and restricted to the immediate bothrial area. In a limited group of mirids the bothrium is elevated and tuberculate, and the trichoma is absent (fig. 9) or poorly developed (fig. 10).

*Trichobothrial Number and Arrangement.* Figures 13 and 14 give a generalized picture of the femoral trichobothria in the Miridae and a numbering scheme used to identify them for establishing homologies among the various taxa. In certain groups, such as the Monaloniini, Odoniellini, and Dicyphinae (and certain genera with greatly modified patterns such as *Coquillettia* and *Pangania*), no attempt has been made to establish homologies. Also, the trichs of the mesofemora are not numbered for most taxa, as the number is invariably six. Trichs without trichomae and not obviously homologous with those in the primitive pattern are given letter designations. In some groups trichobothria in excess of the putative primitive number are given letter designations in conjunction with the numbered trich to which they are proximate; trichobothrium "la" of the metafemur, however, appears to

be present in the primitive complement. The criteria used in determining homologies include trichobothrial location, trich length, and bothrial development.

Six mesofemoral trichobothria occur in all mirid subfamilies except the Isometopinae and Dicyphinae (see below for discussion of relationships of Dicyphinae) and this number can therefore at least tentatively be considered as primitive. The mesofemoral trichobothria are arranged in a more or less linear fashion and are always ventral or nearly so. Often the most distal trich (1) is on the inner surface of the femur, in contrast to the rest; this is usually the first trich to be lost.

The number of metafemoral trichobothria varies more than that of the mesofemora, although a recognizable pattern does exist. As is easily seen in figure 7, there is usually a pair of quite long trichs (2 and 3) situated laterodistally on the metafemur. The orientation of these is strongly outward in most cases. Often there is a single trichobothrium (1) situated distally on the inner surface of the femur, very near the tibial articulation, analogous to mesofemoral trichobothrium number 1. The remaining trichobothria tend to be ventral as on the mesofemur, arranged in a more or less linear fashion. The most common number of trichobothria on the metafemur appears to be eight, at least in what are currently thought of as the more primitive taxa (e.g., Cylapinae) and thus this can tentatively be considered the primitive number. This idea is supported by the reduced trichobothrial numbers found in many obviously specialized taxa, particularly those showing ant mimicry.

#### SUMMARY OF THE TRICHOBOTHRIAL CONDITION

**Bryocorinae.** Two distinct groups are represented: (1) Bryocorini and (2) Monaloniini and Odoniellini, the former with high trichobothrial numbers and primitive pattern (of type found in majority of mirid taxa), recessed bothrium, and well-developed trichoma; the last two with trichobothrial numbers of six or fewer on the mesofemora and metafemora, all trichobothria more or less ventral, bothrium tuberculate, and trichoma absent; affinities of two groups as indicated below.

Bryocorini (figs. 7, 8, 15, 16). Six mesofemoral, eight metafemoral trichobothria, arrangement and number apparently quite constant throughout tribe; trichobothrial pattern primitive; bothrium often deeply recessed; trichoma well developed; not appearing closely related to Monaloniini and Odoniellini on basis of trichobothrial structure.

*Taxa Examined.* *Pycnoderes* sp., *Eccritotarsus* sp., *Sinervus* sp., *Pachymerocerus pilosus* Carvalho.

Monaloniini (figs. 9, 17, 18). One to six mesofemoral, one to seven metafemoral trichobothria, all ventral in orientation, proximal to trochanter in taxa with strongly reduced numbers (i.e., *Helopeltis*, *Monalonia*); bothrium tuberculate, trichoma absent; relationships with Odoniellini and Dicyphinae.

*Taxa Examined.* *Helopeltis* sp., *Monalonia* sp., *Pachypeltis* sp.

Odoniellini (figs. 19, 20). Four mesofemoral, five metafemoral trichobothria, all ventral in orientation; bothrium tuberculate; trichoma absent; relationships with Monaloniini and Dicyphinae.

*Taxon Examined.* *Parabryocoropsis* sp.

**Cylapinae.** Taxa examined with uniformity of trichobothrial structure at tribal level, all with primitive number and pattern; bothrium slightly or not at all recessed; trichoma well developed; possible relationships indicated below.

Cylapini (figs. 11, 23, 24). Six mesofemoral, eight metafemoral trichobothria; bothrium slightly recessed; trichoma strongly developed, spicules without definite orientation, of type also found in Deraeocorini.

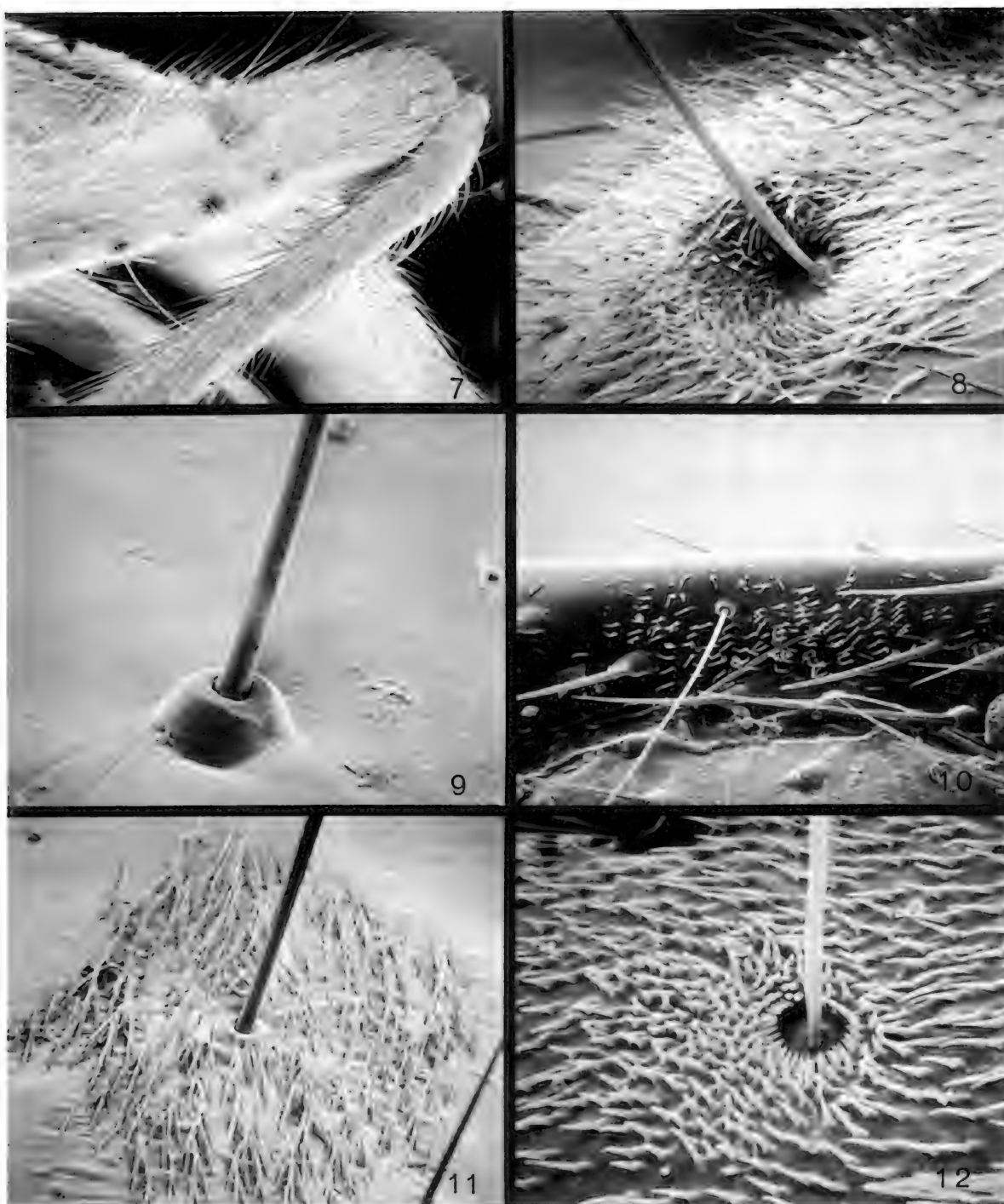
*Taxa Examined.* *Cylapus* spp.

Fulviini (figs. 12, 25, 26). Six mesofemoral, eight metafemoral trichobothria; bothrium slightly recessed; trichoma well developed, asymmetrical, spicules with definite orientation, similar to some Mirinae.

*Taxa Examined.* *Fulvius* spp.

**Deraeocorinae.** Great variability in numbers of trichobothria among tribes; some taxa with trichobothria with and without trichomae; close relationships with other taxa not obvious, although trichoma type generally similar to that of Cylapini.

Deraeocorini (figs. 30, 35, 36). Six mesofemoral, six metafemoral trichobothria; bothrium slightly recessed; trichoma strongly de-



FIGS. 7-12. Trichobothria of Miridae, scanning electron photomicrographs. 7. *Pachymerocerus pilosus* metafemur, 200X. 8. *Idem*, 1350X. 9. *Pachypeltis* sp., 220X. 10. *Cyrtopeltis ebaeus*, 650X. 11. *Cylapus* sp., 1050X. 12. *Fulvius* sp., 2200X.

veloped, spicules long, without definite orientation.

*Taxa Examined.* *Deraeocoris ostentans* (Stål), *Deraeocoris* sp.

Hyaliodini (figs. 37, 38). Two mesofemoral, four metafemoral trichobothria with trichomae, three mesofemoral, three metafemoral trichobothria without trichomae; bothrium only slightly recessed; trichoma strongly developed for certain trichobothria, spicules long, without definite orientation, similar to type in *Deraeocoris*.

*Taxon Examined.* *Hyaliodes vitripennis* (Say).

Surinamellini (figs. 39, 40). Three mesofemoral, four metafemoral trichobothria; trichs short; bothrium similar to *Deraeocoris*; trichoma similar to *Deraeocoris* but less extensive.

*Taxon Examined.* *Nicostratus diversus* Distant.

Teratophylini (figs. 41, 41). Four mesofemoral, three metafemoral trichobothria; bothrium and trichoma appearing similar to *Deraeocoris*.

*Taxon Examined.* *Teratophylum* sp. (no SEM examination).

**Dicyphinae** (figs. 10, 21, 22). Trichobothria ventral in orientation (four mesofemoral, five metafemoral); bothrium tuberculate; trichoma poorly developed and diffuse; relationships with Monaloniini and Odoniellini on basis of trichobothrial number and arrangement and bothrial structure. (Note: Species of the genus *Rhodocoris* Schmitz, 1970, have six mesofemoral and eight metafemoral trichobothria, suggesting a closer relationship with the Bryocorini than with the Dicyphinae, where they have been placed by Schmitz; this relationship is also indicated by the structure of the pretarsus.)

*Taxa Examined.* *Cyrtopeltis ebaeus* Odhiambo, *Dicyphus* sp.

**Isometopinae** (figs. 27-29). Trichobothrial number strongly reduced (two mesofemoral, three metafemoral); bothrium recessed; trichoma well developed, compact; relationships not obvious, form of bothrium similar to Orthotylinae and Phylinae, trichobothrial number and arrangement similar to Teratophylini.

*Taxa Examined.* *Corticoris signatus* (Heidemann), *Heidemania cixiiformis* Uhler, *Myioma* sp. (examined with SEM).

**Mirinae.** Many taxa with trichobothrial num-

ber higher than primitive number, all trichobothria with trichomae (compare with Phylinae); bothrium weakly or not at all recessed; trichoma very weakly developed, spicules very short and only slightly denser than spicules of adjacent cuticle (fig. 33); relationships obscure, possibly an advanced type with reduction of trichoma and increase in trichobothrial number, or a primitive bothrium-trichoma type with an independent increase in trichobothrial numbers over the primitive complement (i.e., six mesofemoral, eight metafemoral).

Herdoniini (figs. 31, 43, 44). Seven mesofemoral, seven metafemoral trichobothria; bothrium indistinct, trichoma absent or poorly developed (Note: The actual numbers of trichobothria indicated for this taxon may not be accurate in that in the species examined it was virtually impossible to differentiate between trichobothria and other long erect setae on the femora; because of this the trichobothria have not been numbered in figs. 43 and 44).

*Taxon Examined.* *Paraxenetus guttulus* (Uhler).

Hyalopeplini (figs. 32, 45, 46). Eight mesofemoral, nine metafemoral trichobothria; bothrium weakly recessed; trichoma moderately developed in immediate area of bothrium.

*Taxon Examined.* *Hyalopeplodes* sp.

Mirini (figs. 33, 47-48). Seven mesofemoral, seven to nine metafemoral trichobothria; bothrium not recessed; trichoma obscurely developed in all taxa examined.

*Taxa Examined.* *Phytocoris* sp., *Stenotus nigroquadristriatus* (Kirkaldy), *Taylorilygus voseleri* (Poppius), *Taylorilygus* sp.

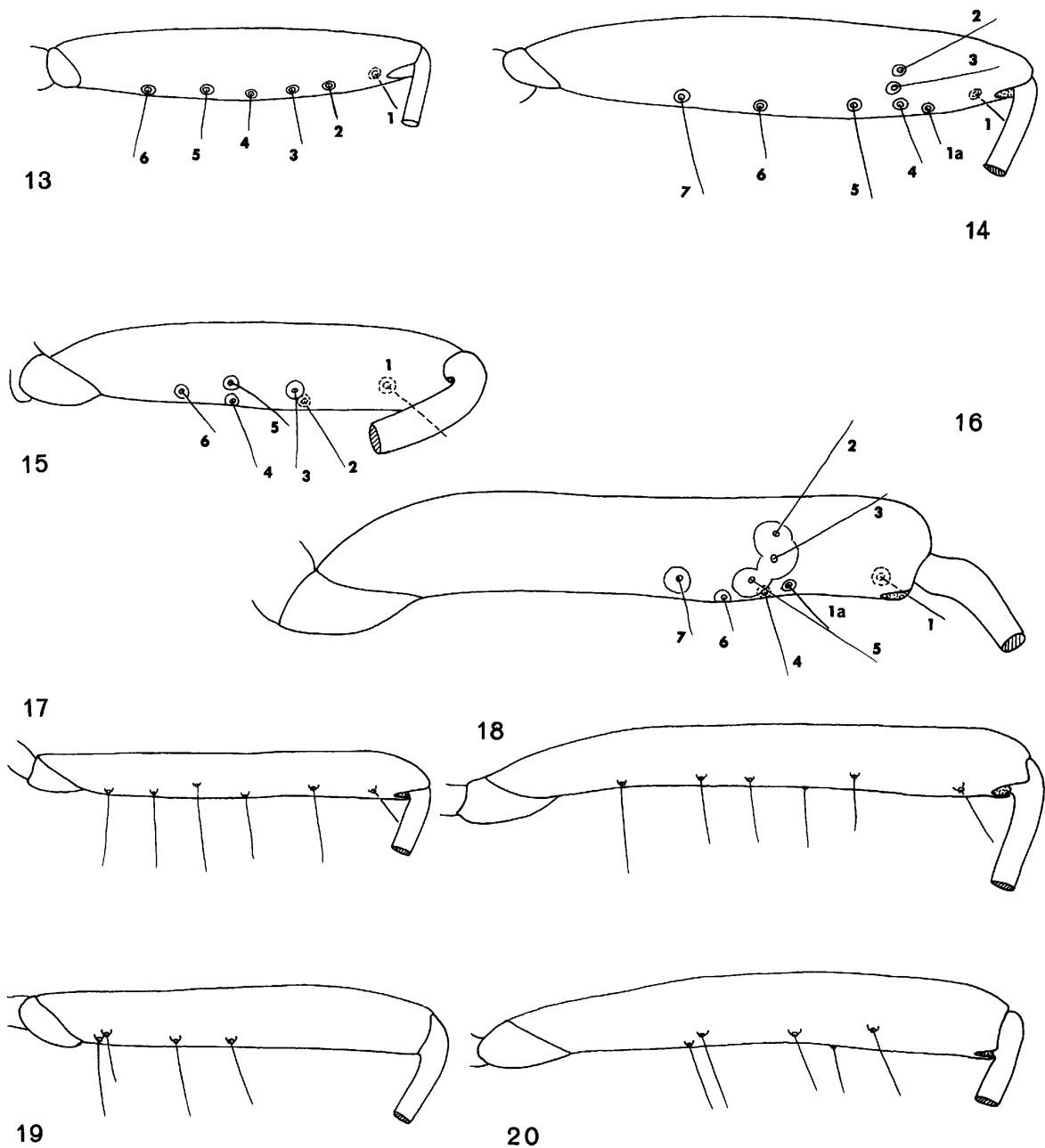
Restheniini (fig. 34). Seven mesofemoral, nine metafemoral trichobothria; trichs relatively short; bothrium flush with surrounding cuticle, not distinctly developed; trichoma obsolete.

*Taxon Examined.* *Prepops insitivus* (Say).

Stenodemini (figs. 49, 50). Five to eight mesofemoral, six to ten metafemoral trichobothria; bothrium flush with surrounding cuticle, not distinctly developed; trichoma similar in form to Mirini (fig. 33).

*Taxa Examined.* *Collaria oleosa* (Distant), *Nabidomiris* sp., *Notostira* sp., *Trigonotylus* sp.

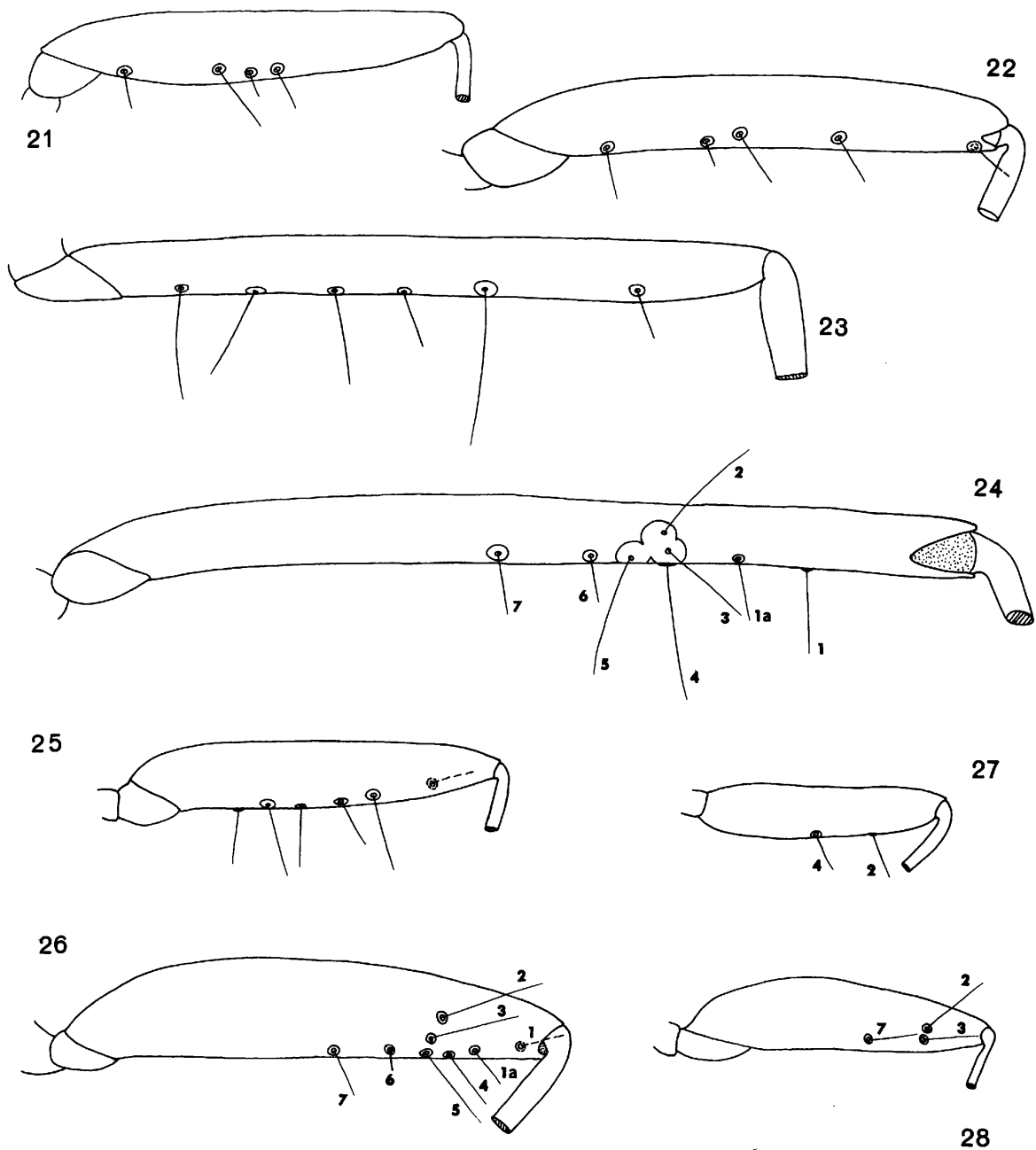
**Orthotylinae.** Trichobothrial number variable, usually not highly reduced (but see Nicho-



FIGS. 13-20. Number and arrangement of trichobothria in Miridae. 13. Hypothetical arrangement of trichobothria on mesofemur. 14. Hypothetical arrangement of trichobothria on metafemur. 15. *Pycnoderes* sp., lateroventral view of mesofemur. 16. *Idem*, lateral view of metafemur. 17. *Pachypeltis* sp., lateral view of mesofemur. 18. *Idem*, lateral view of metafemur. 19. *Parabryocoropsis* sp., lateral view of mesofemur. 20. *Idem*, lateral view of metafemur.

machini), pattern usually of primitive type; bothrium usually recessed; trichoma usually well

developed, compact, although variable in some cases; relationships apparently with Phylinae (al-

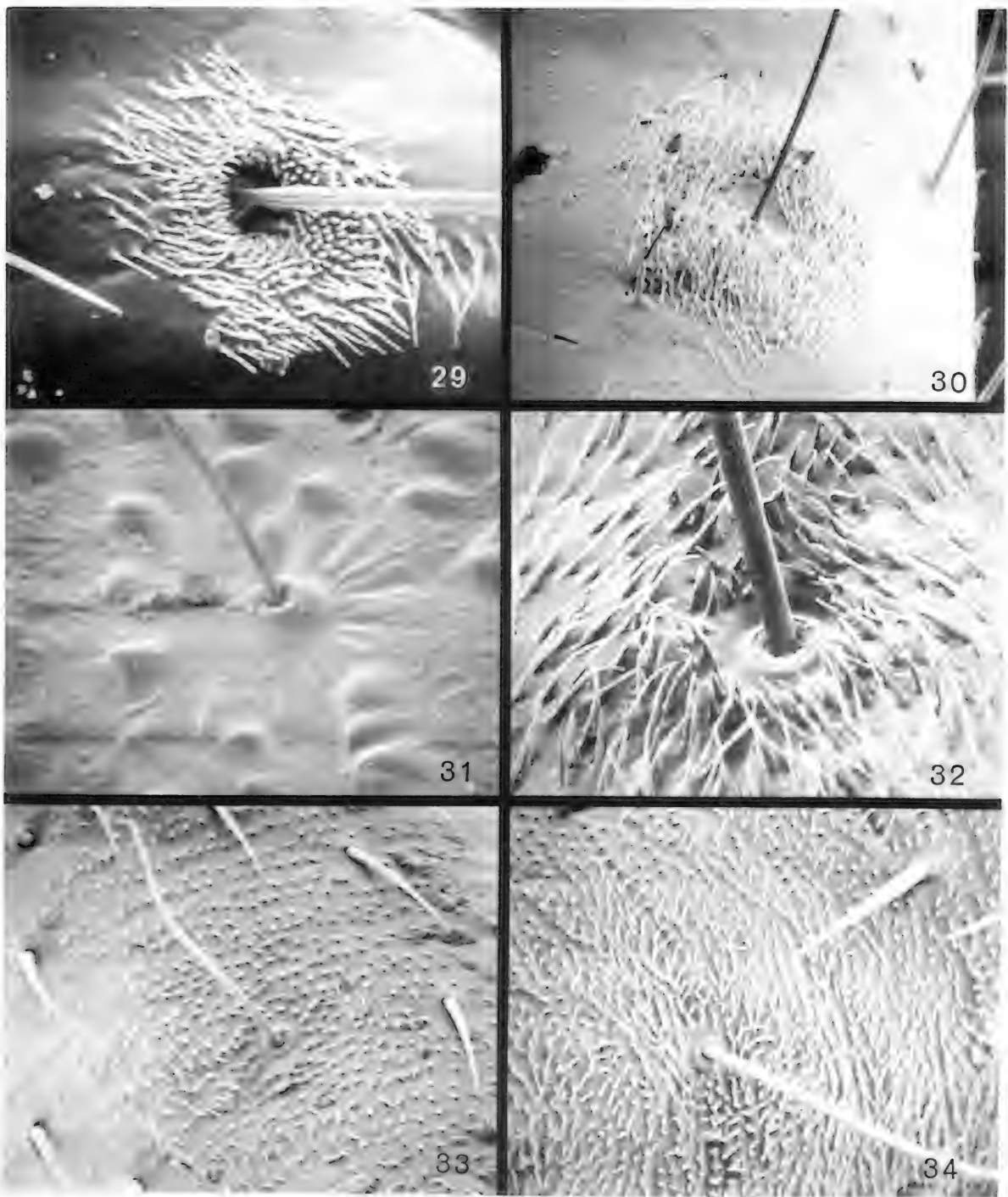


FIGS. 21-28. Number and arrangement of trichobothria in Miridae. 21. *Cyrtopeltis ebaeus*, lateral view of mesofemur. 22. *Idem*, lateroventral view of metafemur. 23. *Cylapus* sp., lateral view of mesofemur. 24. *Idem*, lateroventral view of metafemur. 25. *Fulvius* sp., lateral view of mesofemur. 26. *Idem*, lateroventral view of metafemur. 27. *Myiomma* sp., lateral view of mesofemur. 28. *Idem*, lateroventral view of metafemur.

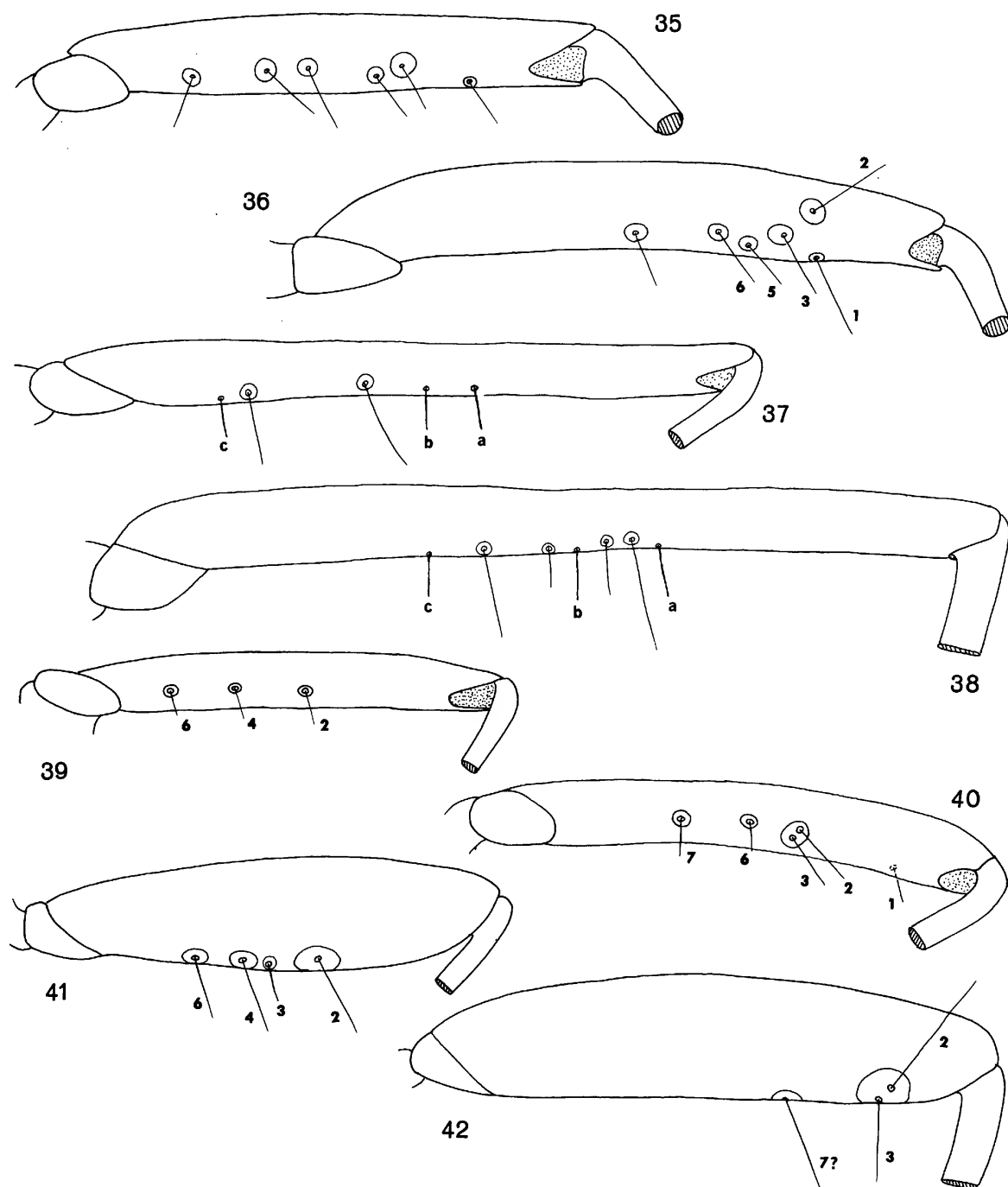
though possibly based on primitive characters).

Halticini (figs. 51, 57, 58). Six mesofemoral,

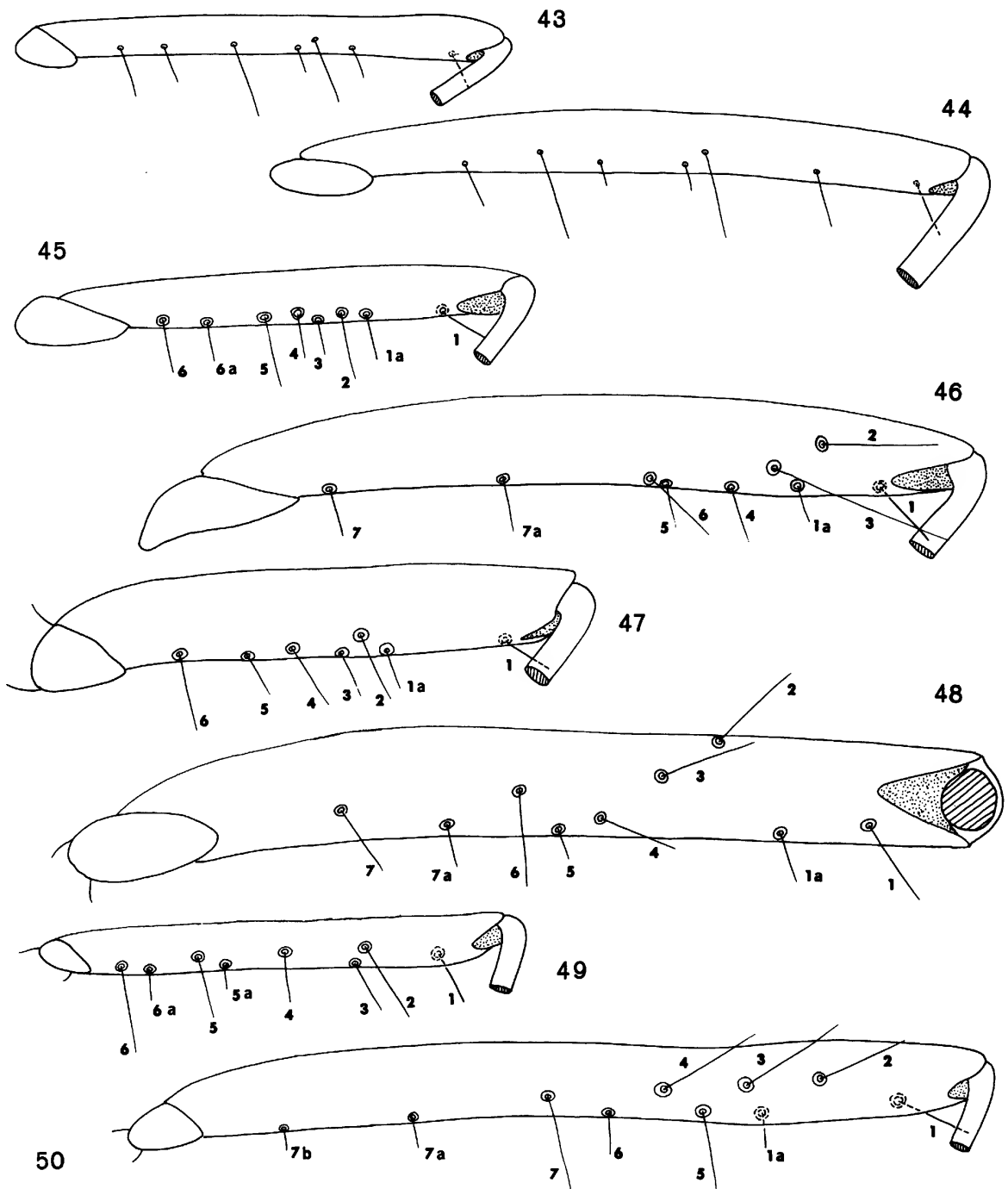
seven metafemoral trichobothria, numbers and arrangement apparently constant within tribe



FIGS. 29-34. Trichobothria of Miridae, scanning electron photomicrographs. 29. *Myiomma* sp., 2000X. 30. *Deraeocoris ostentans*, 950X. 31. *Paraxenetus guttulatus*, 2350X. 32. *Hyalopeplodes* sp., 1000X. 33. *Taylorilygus vosseleri*, 950X. 34. *Prepops insitivus*, 2450X.



FIGS. 35-42. Number and arrangement of trichobothria in Miridae. 35. *Deraeocoris ostentans*, ventral view of mesofemur. 36. *Idem*, ventral view of metafemur. 37. *Hyaliodes vitripennis*, lateroventral view of mesofemur (trichobothria a, b, and c without trichomae). 38. *Idem*, lateral view of metafemur (trichobothria a, b, and c without trichomae). 39. *Nicostratus diversus*, lateroventral view of mesofemur. 40. *Idem*, lateroventral view of metafemur (trichobothrium 1 without trichoma). 41. *Teratophylum* sp., lateral view of mesofemur. 42. *Idem*, lateral view of metafemur.



FIGS. 43-50. Number and arrangement of trichobothria in Miridae. 43. *Paraxenetus guttulatus*, lateral view of mesofemur. 44. *Idem*, lateral view of metafemur. 45. *Hyalopepoides* sp., lateroventral view of mesofemur. 46. *Idem*, lateroventral view of metafemur. 47. *Taylorilygus vosseleri*, lateroventral view of mesofemur. 48. *Idem*, ventral view of metafemur. 49. *Nabidomiris* sp., lateroventral view of mesofemur. 50. *Idem*, lateroventral view of metafemur.

and probably primitive for subfamily; bothrium recessed; trichoma well developed, compact.

*Taxa Examined.* *Halticus* sp., *Labops burmeisteri* Stål, *Labops hirtus* Knight.

Nichomachini (figs. 59, 60). Four mesofemoral, four metafemoral trichobothria; bothrial structure uncertain, trichoma either very compact or poorly developed (no SEM examination); relationships not obvious.

*Taxon Examined.* *Nichomachus sweeti* Schuh.

Orthotylini (figs. 52-54, 61-64). Trichobothrial number often exceeding primitive number for subfamily, but some trichobothria lacking trichomae (five to six mesofemoral with trichoma, five to seven metafemoral with trichoma); bothrium recessed; trichoma usually well developed, compact (but see *Sericophanes*, fig. 54).

*Taxa Examined.* *Carvalhomiris* sp., *Felisacodes bryocorina* (Poppius), *Sericophanes* sp.

Phylinae. Trichobothrial number usually high, pattern of primitive type, some taxa with trichobothria without trichomae; bothrium usually recessed (but see some *Hallodapini*); trichoma usually present, well developed and compact; appearing most closely related to Orthotylinae in trichobothrial structure, but possibly on the basis of primitive characters.

Hallodapini (figs. 55, 56, 65-68). Trichobothrial number (five to six mesofemoral, four to seven metafemoral) and length variable, showing tendency for reduction in both characters; bothrium sometimes recessed with well-developed trichoma (*Acrorrhinium*, *Hallodapus*) sometimes flush with surrounding cuticle and with poorly developed or obsolete trichoma (*Coquillettia*, *Pangania*).

*Taxa Examined.* *Acrorrhinium brincki* Carvalho and Becker, *Coquillettia* sp., *Hallodapus quadrimaculatus* Schuh, *Pangania fasciatipennis* Poppius.

Leucophoropterini (figs. 69-73). Trichobothrial number (six mesofemoral, seven metafemoral) and arrangement primitive for subfamily; bothrium recessed; trichoma well developed, compact, some genera (see *Tytthus*) with trichobothria without trichomae.

*Taxa Examined.* *Leucophoroptera* sp., *Tytthus alboornatus* Knight.

Phylini (figs. 74-77, 79-82). Trichobothrial number (five to six mesofemoral with trichoma,

seven to eight metafemoral with trichoma) and pattern generally primitive for subfamily, some genera with trichobothria without trichomae; bothrium recessed; trichoma well developed, compact.

*Taxa Examined.* *Austropsallus drakensbergensis* Schuh, *Austropsallus helichrysi* Schuh, *Ellenia obscuricornis* (Poppius), *Eminoculus drosanthemi* Schuh.

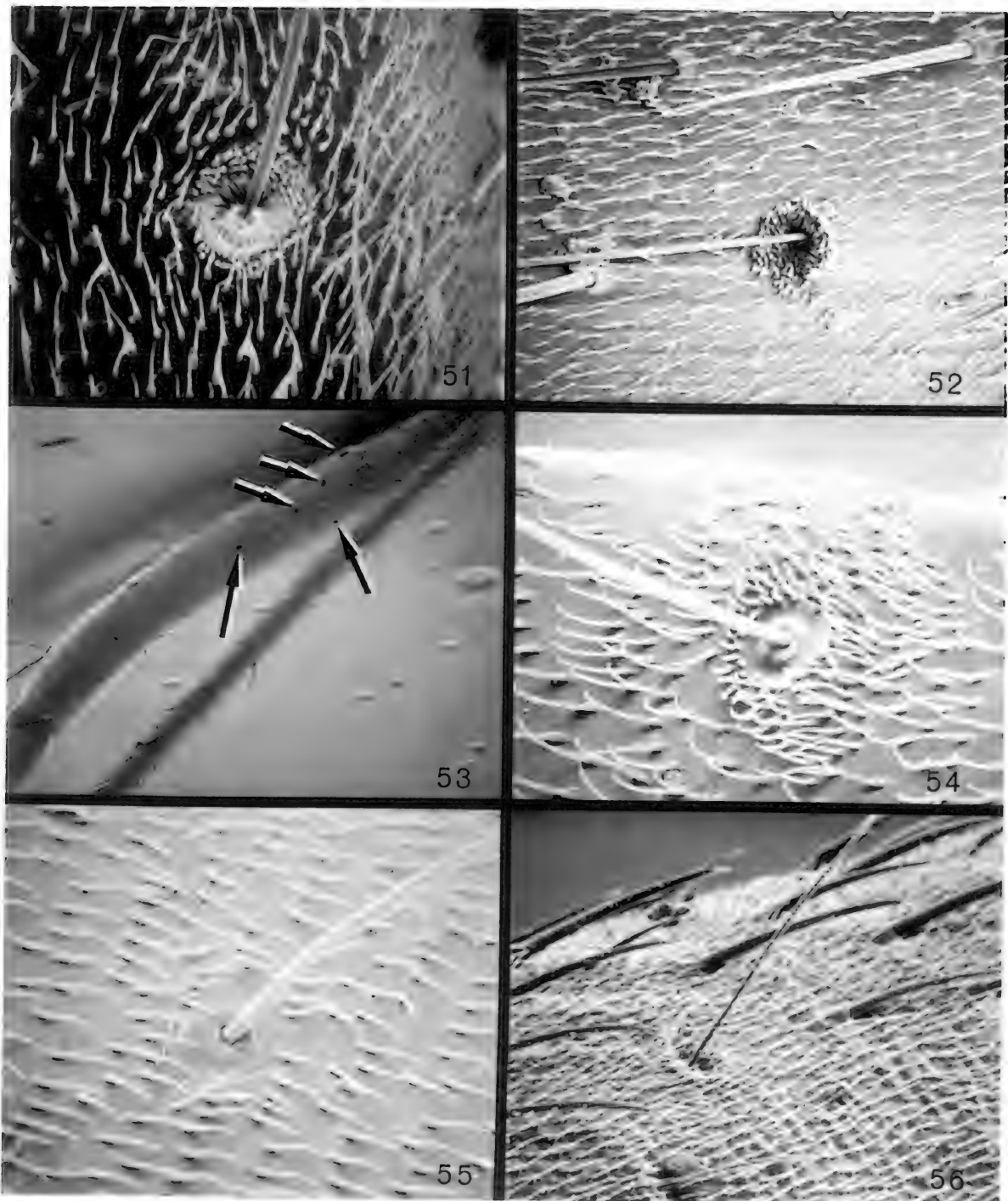
Pilophorini (figs. 78, 83, 84). Six mesofemoral, seven metafemoral trichobothria, pattern primitive for subfamily; bothrium recessed; trichoma well developed, compact.

*Taxa Examined.* *Paramixia australis* Schuh, *Pilophorus uhleri* Knight.

*Discussion and Phylogenetic Considerations.* Although our understanding of the trichobothria in the Miridae is still limited, some generalizations can be made. Certainly, statements about broad phylogenetic relationships among the Miridae will have to be based on other characters in conjunction with the trichobothria. Nonetheless, patterns of relationship indicated by the trichobothria are apparent, and these seem to be in basic agreement with the affinities previously established using other characters.

Based on the bothrial type, the completely absent or reduced trichoma, and the trichobothrial number and pattern, a relationship is evident between the Monaloniini, Odoniellini, and Dicyphinae. This relationship was mentioned by Cobben (1968), based on the eggs, and is also strongly suggested by the pretarsal structures (Schmitz, 1970; Schuh, 1974, p. 264; Schuh, MS.). That the rather compelling similarities of the Dicyphinae and Monaloniini (and Odoniellini) have not been noted by most earlier authors is certainly a reflection of the fact that most of them were working with temperate faunas and did not have representatives of the Monaloniini or Odoniellini available for examination. A more distant relationship is suggested between the Monaloniini-Odoniellini and the Bryocorini, which have been generally placed in the same subfamily; this idea has been expressed previously by Cobben (1968) based on characters of the eggs.

Although the Bryocorini have a trichobothrial type very similar to the remainder of the Miridae (exclusive of the Monaloniini group), this rela-



FIGS. 51-56. Trichobothria of Miridae, scanning electron photomicrographs. 51. *Halticus* sp., 1930X. 52. *Carvalhomiris* sp., 950X. 53. *Idem*, lateroventral view of metaleg, 65X. 54. *Sericophanes* sp., 2100X. 55. *Coquillettia* sp., 2100X. 56. *Pangania fasciatipennis*, 1080X.

tionship is not so obvious based on other structures, particularly the pretarsus; neither is the relationship clarified in any way by the trichobothrial information presently available, because the type of pattern in the Bryocorini is almost certainly primitive for the Miridae in general, and no relationships can thus be postulated. Obviously, derived characters will have to be sought in order to determine the relationships between the Bryocorini and the other non-Monaloniini group mirids.

A certain homogeneity of structure does exist among the remaining groups of Miridae (i.e., Cylapinae, Deraeocorinae, Isometopinae, Mirinae, Orthotylinae, and Phylinae). However, our understanding of variation within the family as a whole limits the generalizations that can be made to those that follow.

The variation in trichobothrial numbers is toward reduction. This is evidenced in the Isometopinae, Termatophylini, Surinamellini, some Hallodapini, and possibly others. No obvious phyletic or adaptive trends are recognizable at present, however. Such groups as the Surinamellini and Hallodapini are obviously specialized within their individual phyletic lines, in these cases for ant mimicry. At least in the case of the Hallodapini, some of the more specialized genera such as *Pangania* and *Coquillettia* show a reduced trichobothrial number and trich length as well as a poorly developed trichoma, compared with what might be regarded as more generalized taxa, such as *Hallodapus* and *Acrorhynchium*, which have a primitive trichobothrial number and pattern and a well-developed trichoma. Groups such as the Isometopinae possess primitive characters (e.g., ocelli), but are probably specialized with respect to the trichobothria, having very low numbers.

An apparent increase in trichobothrial number is seen in some taxa, especially the Mirinae. In this case, all the trichobothria have trichomae. It does not appear that the trichobothria of the Mirinae, which are in excess of the numbers found in other taxa such as the Cylapinae, have been lost in the latter but rather that they have been independently evolved in the former. This conclusion is based on the nearly constant pattern of six mesofemoral and eight (or seven)

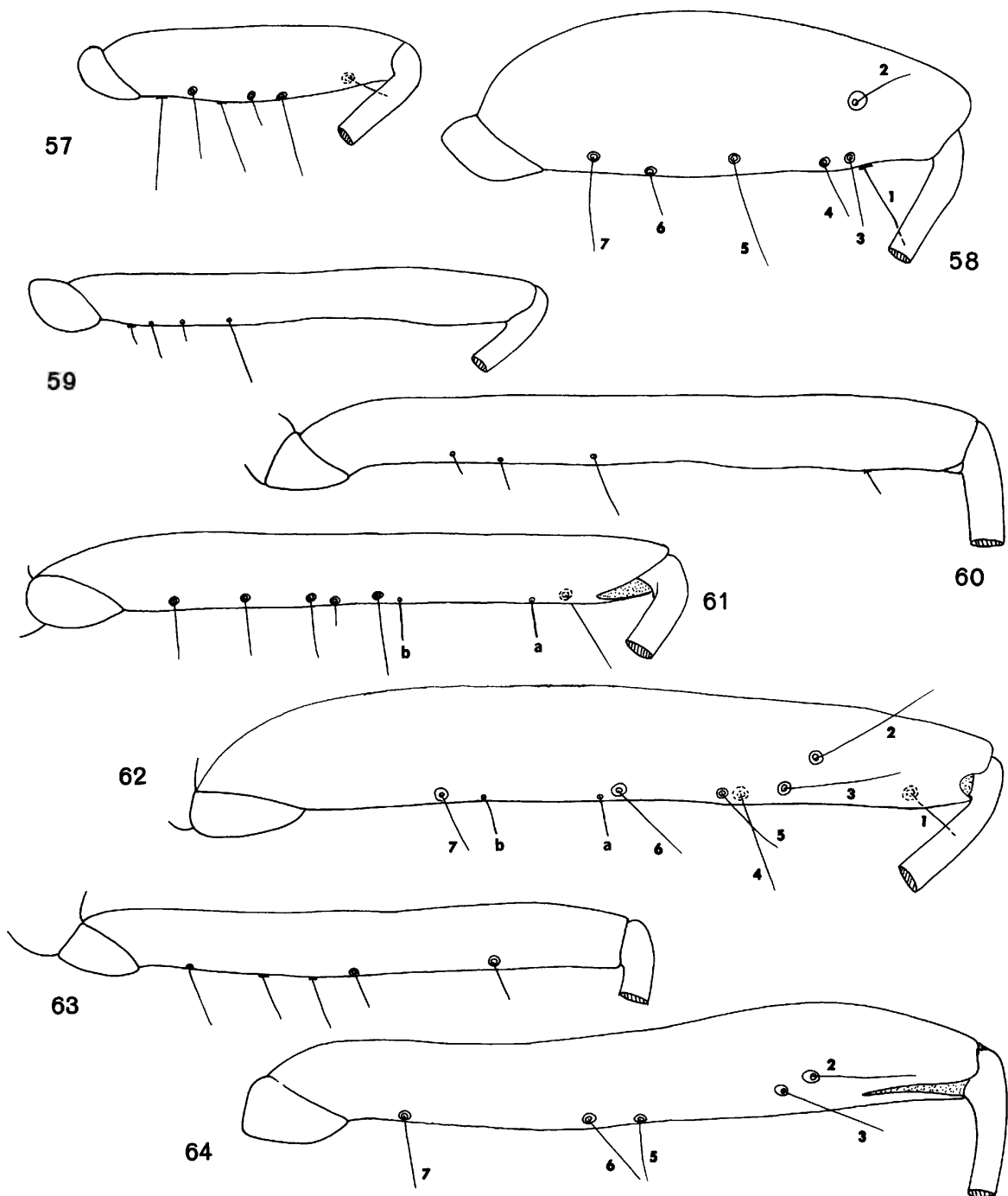
metafemoral trichobothria in the remaining subfamilies.

In contrast to the Mirinae, in *Austropsallus* and *Ellenia* (Phylinae), *Hyaliodes* (Deraeocorinae), and certain other genera, some of the trichobothria lack trichomae (compare figs. 74 and 75 for *Austropsallus*); *Hyaliodes* also lacks several of the trichobothria present in the primitive pattern for the family. It is impossible to say at the moment whether those trichobothria without trichomae have lost the structure, or are derived independently from setae not homologous with the standard complement of trichoma-bearing trichobothria found in most Miridae, although it seems likely that both may have occurred.

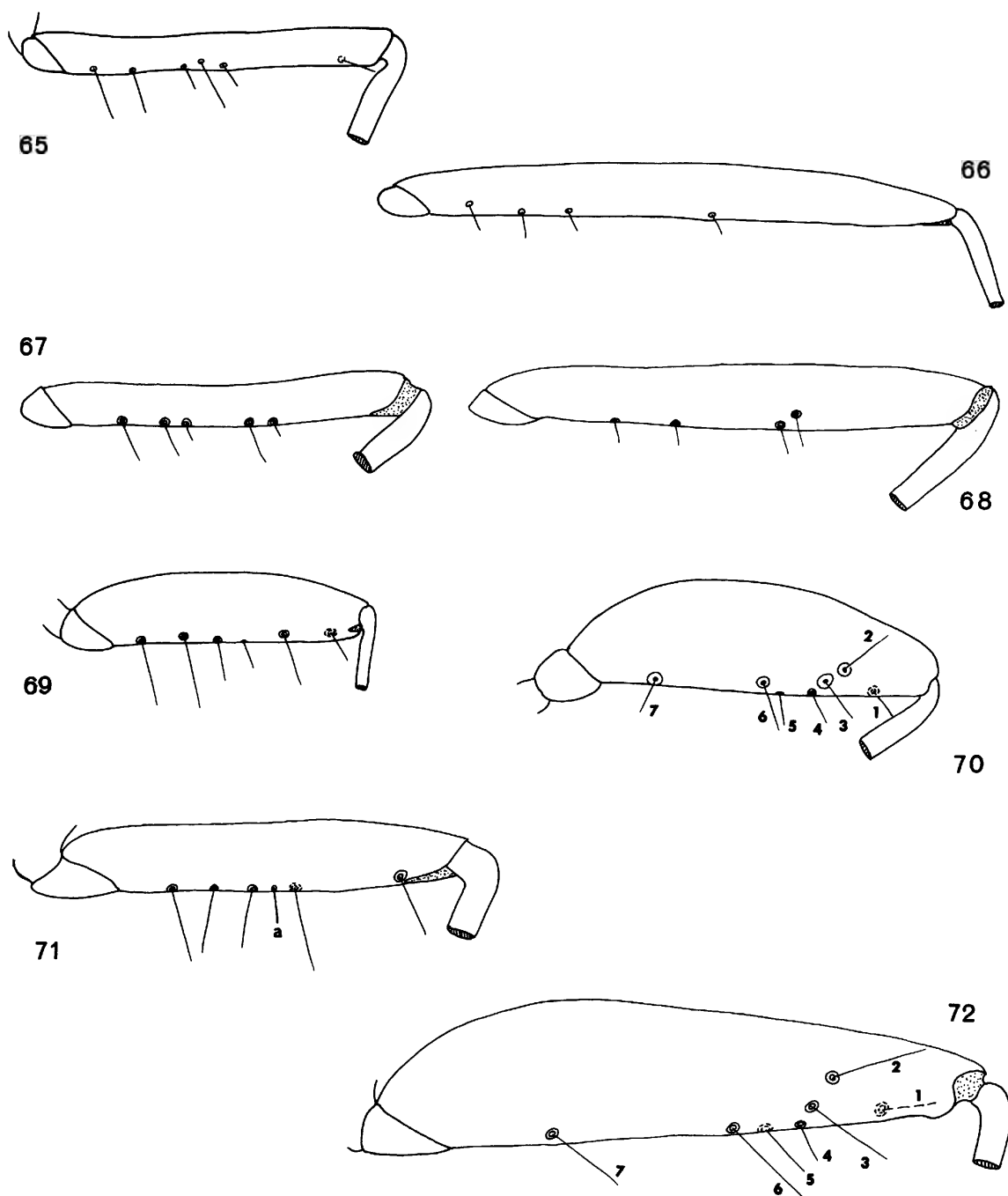
Patterns of development of the trichoma and bothrium make it difficult to postulate relationships, as suggested by the following examples. In the Cylapinae, Deraeocorinae, and Mirinae the bothrium is not recessed and the trichoma is often diffuse; in the Mirinae the trichoma is not easily recognizable as such, except under close examination. Within the Cylapinae, however, those Fulviini examined have trichomae similar to some Mirinae, and the Cylapini similar to those known in the Deraeocorinae.

In the Isometopinae, Phylinae, and Orthotylinae the tendency is for the bothrium to be from slightly to deeply recessed into the surrounding cuticle, and for the trichoma to be a compact, definitely oriented group of spines, easily distinguished from the investing setae or spicules on the adjacent cuticle. In the Hallodapini (Phylinae), an apparently advanced group, the bothrium is not recessed and the trichoma is absent or poorly developed in some genera as the result of reduction. This appears to have occurred several (possibly many) times, in the Hallodapini and other taxa, making the use of bothrial-trichomal characters difficult for evaluating relationships.

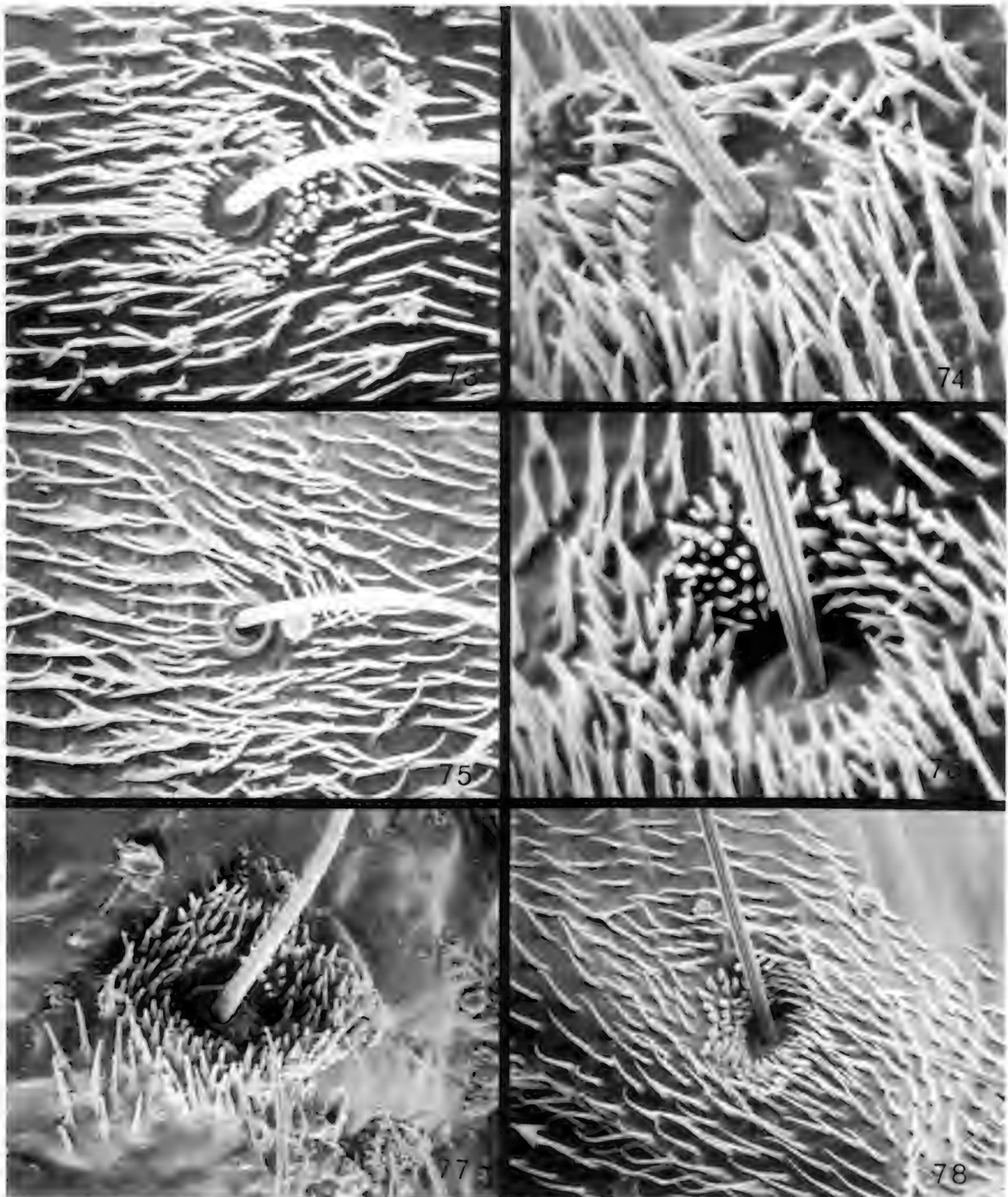
Probably the most important conclusions that can be drawn from the available data are that for the Hemiptera in general trichobothria have almost certainly evolved several times independently. As with the Arachnida, the Hemiptera seem to be disposed to the multiple evolution of these structures.



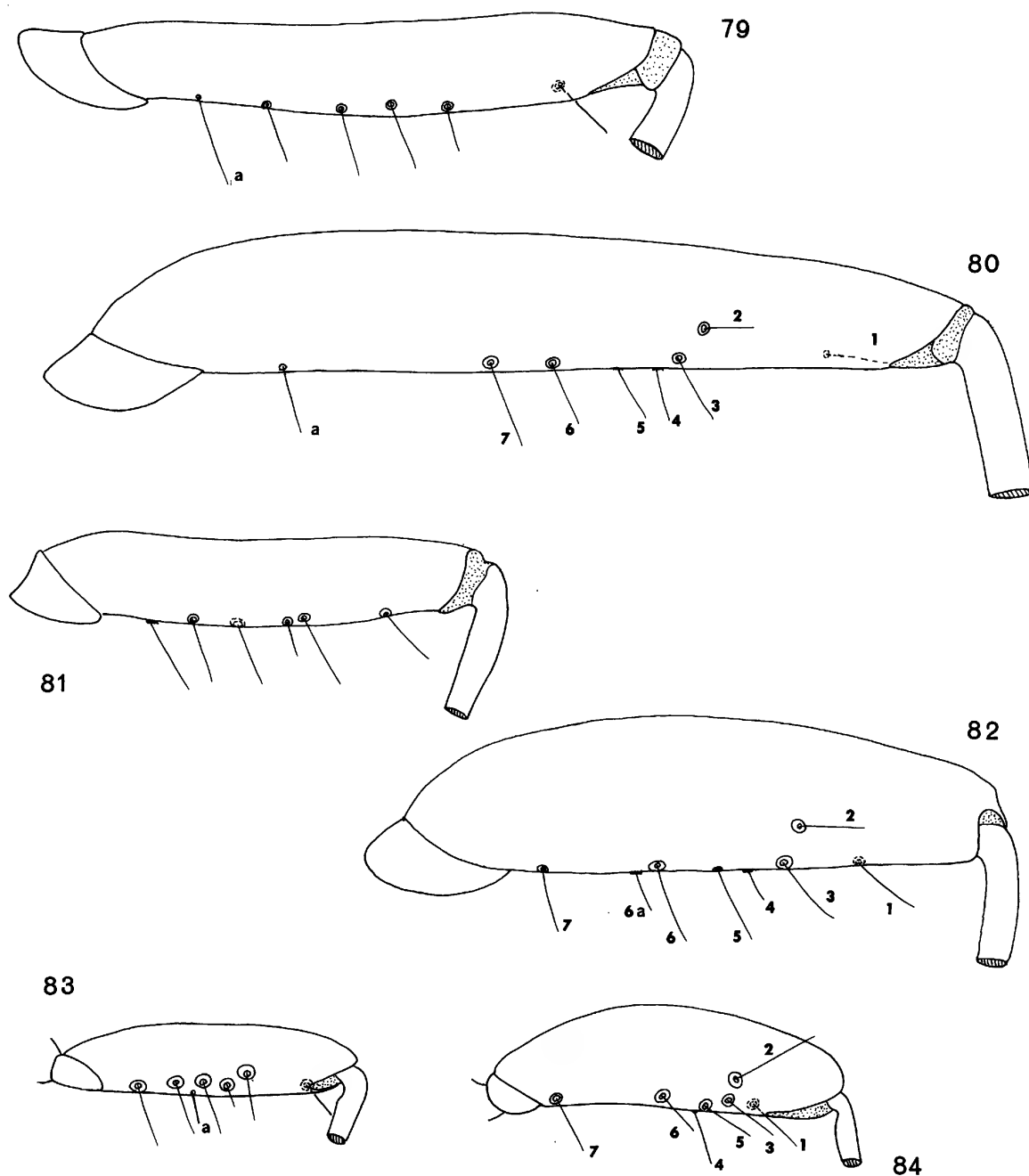
FIGS. 57-64. Number and arrangement of trichobothria in Miridae. 57. *Halticus* sp., lateral view of mesofemur. 58. *Idem*, lateral view of metafemur. 59. *Nichomachus sweeti*, lateral view of mesofemur. 60. *Idem*, lateral view of metafemur. 61. *Carvalhomiris* sp., lateroventral view of mesofemur (trichobothria a and b without trichomae). 62. *Idem*, lateroventral view of metafemur (trichobothria a and b without trichomae). 63. *Sericophanes* sp., lateral view of mesofemur. 64. *Idem*, lateroventral view of metafemur.



FIGS. 65-72. Number and arrangement of trichobothria in Miridae. 65. *Coquillettia* sp., lateral view of mesofemur. 66. *Idem*, lateral view of metafemur. 67. *Pangania fasciatipennis*, lateral view of mesofemur. 68. *Idem*, lateral view of metafemur. 69. *Leucophoroptera* sp., lateral view of mesofemur. 69. *Leucophoroptera* sp., lateral view of mesofemur. 70. *Idem*, lateral view of metafemur. 71. *Tytthus alboornatus*, lateral view of mesofemur (trichobothrium a without trichoma). 72. *Idem*, lateral view of metafemur.



FIGS. 73-78. Trichobothria of Miridae, scanning electron photomicrographs. 73. *Leucophoroptera* sp., 2600X. 74. *Austropsallus drakensbergensis*, 4800X, with trichoma. 75. *Idem*, 2350X, without trichoma. 76. *Ellenia obscuricornis*, 5000X. 77. *Eminoculus drosanthemi*, 2400X. 78. *Paramixia australis*, 2000X.



FIGS. 79-84. Number and arrangement of trichobothria in Miridae. 79. *Austropsallus helichrysi*, lateral view of mesofemur (trichobothrium a without trichoma). 80. *Idem*, lateral view of metafemur (trichobothria 1 and a without trichomae). 81. *Ellenia obscuricornis*, lateral view of mesofemur (the trichobothria and some spines on the femora are situated on large black spots). 82. *Idem*, lateral view of metafemur. 83. *Paramixia australis*, lateroventral view of mesofemur. 84. *Idem*, lateroventral view of metafemur.

Within the Miridae, the femoral trichobothria represent an autapomorphic (uniquely derived) character and the family forms a monophyletic group with the inclusion of the Isometopinae. Analysis of trichobothrial patterns and numbers suggests that at least two arrangements have evolved: (1) the Monaloniini-type, with from one to six trichobothria situated ventrally or nearly so on the mesofemora and metafemora, a tuberculate bothrium, and no trichoma (or with the trichoma very poorly developed) and (2) the Bryocorini-Cylapini type with six mesofemoral and eight (or fewer) metafemoral trichobothria, a flush or recessed bothrium, and a well-developed trichoma. In the latter case all the structures have been reduced in number or degree of development several times. The lack of a trichoma in the Monaloniini-group might suggest that it possesses the more primitive trichobothrial condition, but the tuberculate bothrium may be an advanced type. A larger complex of characters will have to be analyzed in order to clarify this situation. It is possible that neither group possesses the ancestral trichobothrial pattern or number, but substantiation of this will require further analysis.

The information content of future taxonomic work on the Miridae can be increased by inclusion of data on the trichobothria. At present, an understanding of variability is needed, especially in taxa such as the Hallodapini where a wide range of number and structure is known to exist. Such contributions will certainly aid our phylogenetic studies of the family in the long run.

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